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SHORT COMMUNICATIONS

Extra nest site occupancy by Tree Swallows: Do floaters avoid nest sites near settled pairs?—Tree Swallows (*Tachycineta bicolor*) are secondary hole-nesters for whom suitable cavities are a limiting resource (Holroyd 1975, Stutchbury and Robertson 1985). Despite nest site shortage, more than one cavity may be occupied by a single breeding pair (Rendell and Robertson 1994). Because Tree Swallows are single-brooded and generally monogamous (Robertson et al. 1992, but see Hussel 1983), the second site often goes unused. Occupancy of extra nest sites (ENSs) is therefore puzzling.

In this study we tested the hypothesis that ENS occupancy by Tree Swallows results from avoidance by floaters of nest sites near settled pairs. To date, most explanations of this behavior have assumed that a differential cost to defending the second site exists,.and all have focused on benefits arising from its successful defense (Kendeigh 1941, Harris 1979, Robertson and Gibbs 1982, Muldal et al. 1985, Finch 1990, Dunn and Hannon 1991, Rendell and Robertson 1994). An alternative explanation is that floaters avoid or reject nest sites too close to already settled pairs. Residents may then occupy the extra sites without any increase in their total defense costs. That is, an ENS may be nothing more than a convenient perch from which to observe the primary site. The "avoidance hypothesis" sees ENS occupancy as an artifact of floater behavior rather than as resulting from the resident pair's defense and predicts that floaters will not make use of the nest sites in question even if the residents' defense radius is reduced. The hypothesis was noted in passing by Muldal et al. (1985) but has never been tested.

The avoidance hypothesis gains credibility from the observation that floaters in some Tree Swallow populations reject nest boxes placed in wooded areas or near forest edges (Harris 1979, Rendell and Robertson 1990, but see Erskine and McLaren 1976, Peterson and Gauthier 1985). The selectivity may reflect a risk at those nest boxes of egg destruction and nest site usurpation by House Wrens (*Troglodytes aedon*, Rendell and Robertson 1990) or a need for an open area nearby for foraging (Munro and Rounds 1985). If Tree Swallows are prepared to reject an otherwise suitable nest box because of its proximity to a forested area, might they also do so because of proximity to breeding conspecifics?

Floaters rejecting nest sites may lose breeding opportunities. Estimates of adult annual mortality in Tree Swallows range from 40–60% (Chapman 1955, Houston and Houston 1987) so delaying reproduction is risky. If Tree Swallows do avoid or reject nest sites near settled pairs, failure to do so must entail costs similar in magnitude to those of wren activity. This seems unlikely. Anecdotal accounts of Tree Swallows raising broods in nest boxes 1 m apart (Harris 1979) and even of two females laying in the same nest box (Quinney 1983, Muldal et al. 1985, Rendell 1992) suggest that floaters will breed near conspecifics rather than not breed at all.

To test the avoidance hypothesis, we arranged nest boxes in pairs and visually separated half those pairs with sheets of chipboard. Early in the season, breeding Tree Swallows defend their nest sites by spending the majority of their time perched at or near their nest holes (Leffelaar and Robertson 1984, Stutchbury and Robertson 1987a). Our visual barriers therefore made defense of a second box more difficult. Floaters locate unoccupied nest sites from the air and would be able to see both the unoccupied nest box and its proximity to an occupied box. If floaters avoid nest sites because of their proximity to already settled birds then barriers should have no effect. But, if defense of the extra nest box is important, then floaters should settle more often where barriers are present, i.e., we should observe two pairs of Tree Swallows breeding in adjacent nest boxes when barriers are present. As argued

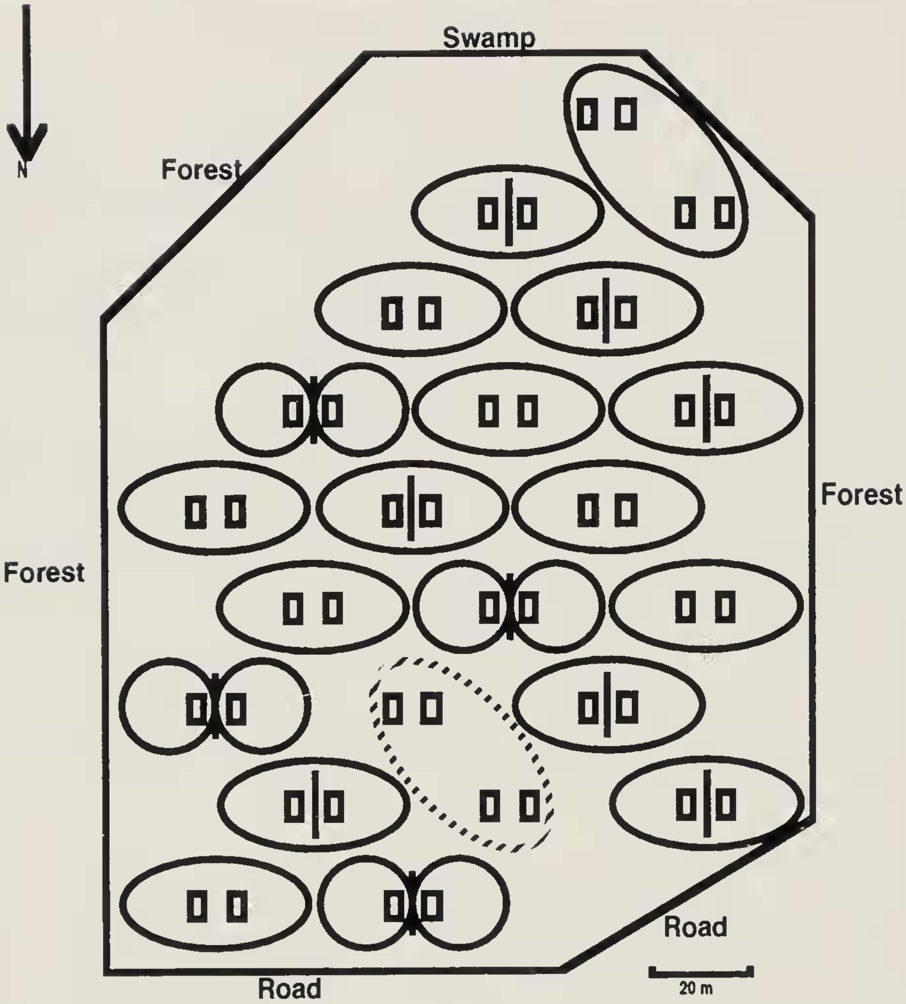

FIG. 1. Diagram of the Tree Swallow grid showing the arrangement of nest boxes (rectangles) and barriers (short vertical lines separating alternate nest box pairs) and the settlement pattern a day before the first egg was laid. Rings around cells or individual nest boxes indicate the nest boxes occupied by a pair of Tree Swallows and are not intended to delineate accurately the area defended. The dashed line ring around four nest boxes (two cells) circles the nest boxes occupied by a bigamous male; each female occupied one cell. Note that two control cells were occupied by one Tree Swallow pair (top right on the diagram) and that two pairs settled at each of four experimental cells.

above, we felt that the avoidance hypothesis, while plausible, was improbable and predicted that floaters would settle adjacent to a breeding pair more readily when a visual barrier was in place.

To avoid confusion between pairs of breeding Tree Swallows and paired nest boxes, we hereafter refer to the latter as cells.

Methods.—In late April 1991, we erected a grid of 44 nest boxes, arranged in 22 pairs (cells), on a 1.6 ha hayfield in Leed's County, Ontario (Fig. 1). Boxes were placed 1.5 m above the ground on aluminum poles. The two nest boxes of a cell were 8 m apart. Since Tree Swallows from this population normally defend a territory around a nest site of radius 15 m (Robertson and Gibbs 1982), we expected defense of a complete cell (two nest boxes) by each breeding pair. The shortest distance between nest boxes from different cells was 23

TABLE 1

NUMBER OF CONTROL AND EXPERIMENTAL PAIRED NEST BOXES (CELLS) AT WHICH BOTH NEST SITES WERE AND WERE NOT OCCUPIED BY A SINGLE BREEDING PAIR OF TREE SWALLOWS

	Barrier	No barrier
Extra nest site occupation maintained	7	11
Extra nest site occupation not maintained	4	0

m, which is greater than the normal defense radius, so defense of more than one cell by a breeding pair was not expected at either experimental or control cells.

At alternate cells down each row of the grid, we erected sheets of chipboard (1.2 × 2.4 m) between the nest boxes such that, from each nest box, the other, 8 m away, could not be seen. Chipboard sheets were visual barriers which, when present, made defense of both nest boxes in a cell more difficult for a breeding pair. Birds could not perch on the barrier because we put a tight line, strung with plastic drinking straws, about 1 cm above the top of each barrier. We refer to cells with chipboard obstructing the view of the adjacent box as barrier cells. The remaining 11 cells were control cells. Nothing obstructed the view of Tree Swallows perched on nest boxes at control cells.

Erecting barriers after settlement might have caused resident abandonment, so we put them up at the same time as the nest boxes, prior to Tree Swallow settlement. We could not detect any difference in any index of settlement date between control and barrier cells and, therefore, concluded that the presence of barriers did not affect the birds' nest box choice decisions (Mitchell 1992).

Residents were captured using mist nets and box traps (Cohen and Hayes 1984, Stutchbury and Robertson 1986) and marked with unique acrylic wing paint codes. Following banding, settlement and residency were determined using periodic 3–5 min watches at individual nest boxes and by regular examination of nest box contents.

Results.—Many Tree Swallow pairs initially occupied more than one cell. The number of breeding pairs then continued to increase throughout the breeding season until 28 active nests (eggs or nestlings present) were spread across the 22 cells and at least one breeding pair of Tree Swallows was present at every cell on the grid. We therefore had to pick a date on which to compare ENS occupancy frequencies at control and barrier cells. Costs and benefits of a second nest site may change following laying, so we decided to compare those frequencies on 13 May, a day prior to the laying of the first egg on the grid, at which time the grid held 25 active nests. Figure 1 shows the grid settlement pattern on 13 May. Occupancy of both nest boxes of a cell by a single breeding pair of Tree Swallows was significantly less common when a barrier separated the two boxes than at controls (one-way Fisher exact test, $N = 22$, $m = 11,4$, $f = 0$, $P = 0.04$) (Table 1). In fact, there were no cases where the two nest boxes of a cell were occupied by separate pairs of Tree Swallows except where a barrier separated those boxes.

The test is conservative since maintenance of two nest boxes broke down only at barrier cells; in addition, one Tree Swallow pair was still occupying two control cells (four boxes) and a bigamous male was also occupying two control cells, with each female occupying a single cell, at this time (Fig. 1). The bigamous two-cell occupation remained stable for the duration of the breeding season. The two-cell occupation ended when the original female started laying at one cell, whereupon a new Tree Swallow pair settled at the second cell.

This was the twenty-sixth active nest. No Tree Swallow was occupying more than one barrier cell at that time.

Approximately four weeks after the initial settling, females settled at the unused nest boxes at one barrier and one control cell following the hatching of the original females' clutches. These may have been lone females or may have been paired with the original resident male. Only the new females fed the nestlings.

We observed several resident females, at both barrier and control cells, adding nesting material to both nest boxes of cells involved in ENS occupancy. In each instance, though, eggs were laid in only one of the boxes. Where pairs occupied extra nest sites, both residents spent time at each nest box and both responded aggressively to intruders, although it was not possible to determine to which box a threat was perceived.

Discussion.—The lower frequency of ENS occupancy when adjacent nest boxes were separated by a visual barrier permits rejection of the avoidance hypothesis. When the ability of a resident to defend a second nest box was experimentally reduced, floaters settled and bred in boxes 8 m from existing pairs. Floaters may prefer to nest at greater distances from conspecifics, but this preference is not a sufficient explanation for ENS occupancy. It is fair to characterize ENS occupancy as ENS defense.

We emphasize that our result cannot simply be an outcome of barriers causing settling floaters to be unaware of their neighbors or residents to be unaware of a nearby nest box. While territory defense is accomplished through time spent perched at a nest site, floaters searching for nest sites do so by flying through a colony repeatedly (Stutchbury and Robertson 1987b) and thus should be aware of a neighbor's presence. The ability of seven Tree Swallow pairs to maintain two nest boxes despite the presence of a barrier demonstrates that the second box's presence is recognized by the resident pair and that defense is possible.

Rendell and Robertson (1994) found that male Tree Swallows, and possibly females, preferred territories on which a second nest box could easily be defended (because of the proximity of adjacent nest boxes). Mitchell (1992) detected no evidence of preference for control cells by Tree Swallows in his study, but the rapid pace of settlement and our small sample size could have masked such a preference. If a preference did exist, it was not sufficient to induce settling Tree Swallow pairs to reject cells consistently where barriers were present. Therefore, our conclusion remains unchanged: Avoidance by floaters is an insufficient explanation for ENS occupancy by Tree Swallows.

Using model intruders, Robertson and Gibbs (1982) concluded that Tree Swallows defend a circular territory around a primary nest box and occupy additional nest boxes which happen to lie within that radius. That hypothesis has since been refuted by Rendell and Robertson (1994) who found that Tree Swallows occupied nest sites up to 56 m apart. These findings raise a question that has thus far not been addressed: When a resident Tree Swallow is observed responding aggressively to an intruder, how can one determine whether the resident perceives a threat to its primary nest site or to an ENS? Our study succeeds in rejecting the avoidance hypothesis without using observations of aggressive behavior. However, we suspect that distinguishing between two remaining hypotheses will require such observations.

Rendell and Robertson (1994) argued that ENS defense by pairs of Tree Swallows results from an intersexual conflict of interest. Males defend an ENS in hopes of becoming polygynous. Females then defend the same extra site to ensure male monogamy. Rendell and Robertson (1994) could not convincingly reject an alternative hypothesis that Tree Swallow pairs cooperate in defense of an ENS as a site for renesting should their first attempt fail. These hypotheses reflect fundamentally different views of territorial behavior. Not only does the explanation for ENS defense differ, but the perceived relationship between members of the breeding pair differs.

If aggressive behavior can be unequivocally assigned to defense of an ENS, then the two explanations can be distinguished by looking at which sex male and female Tree Swallows defend a second site against. If a polygyny-monogamy conflict is involved, females should respond aggressively to intruding females but ignore or actively encourage intruding males, since settlement by a second male removes the risk of polygyny for the female. Male Tree Swallows' pattern of aggression should be just the opposite. If defense is cooperative, both male and female Tree Swallows should defend an ENS against intruders of either sex.

This distinction was not possible in our study, in which paired nest boxes were only 8 m apart. However, the comparison would be worthwhile when the two nest sites are more widely separated, as in some of the cases reported by Rendell and Robertson (1994) and where floaters have been captured, sexed, and individually marked.

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Swainson's Warblers nesting in early seral pine forests in East Texas.—Swainson's Warbler (*Limnothlypis swainsonii*) breeds locally throughout the southeastern United States on the south Atlantic and Gulf coastal plains, in the southern Appalachians, and on the southern Piedmont Plateau (Meanley 1966). They select areas with low, dense understories (Eddleman et al. 1980, Meanley 1971). Meanley (1945, 1966, 1969) described several habitats of Swainson's Warblers in the eastern coastal plains, and they also have nested in dense rhodendron-laurel thickets in the southern Appalachians (Brooks and Legg 1942). However, there is little information on the specific habitat features which may influence the distribution and abundance of this species, especially in the western portion of its breeding range. In this paper, I report on the first described use of early seral pine forests by Swainson's Warblers nesting in eastern Texas. I compare habitats selected in this study to those previously described and suggest possible relationships between habitat selection and abundance patterns.

I surveyed for Swainson's Warblers from April through June 1992 on the San Jacinto Ranger District, Sam Houston National Forest, San Jacinto County, Texas (95°07'W, 30°30'N). The district consists of approximately 24,000 ha of pine, pine-hardwood, and bottomland hardwood forest of various age classes. The district is managed for timber production, recreation, wildlife, and some oil and mineral extraction. Timber is managed primarily in even-age stands ranging from 4–40 ha on 70-year rotations. Harvest methods include thinning, clearcuts, seed-tree cuts, and shelterwood cuts. Large areas regularly are